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# Injuries on Nautilus Jaws: Implications for the Function of Ammonite Aptychi

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*Abstract.* Documentation of repaired injuries and abnormalities on the jaws of modern nautilus sheds light on the ecology and behavior of these animals. It also helps elucidate the function of ammonite aptychi, which are traditionally interpreted as opercula. We examined 219 pairs of jaws belonging to *Nautilus belauensis*, *N. macromphalus*, *N. pompilius*, and *Allonautilus scrobiculatus*. Abnormalities occur in 68% of the sample and are only present on the lower jaw. The abnormalities consist of 1) repaired fractures, 2) small depressions, 3) radial grooves and ridges, and 4) flexures in the chitin. These abnormalities are either the result of injury or growth pathology. Injuries may be due to accidents during feeding (e.g., biting down on a hard crustacean carapace) or from predatory attacks. Alternatively, they may have been sustained during mating behavior or fighting between males. Most abnormalities occur on the left side of the lower jaw. This may be related to the fact that in male nautilus, the jaws are displaced to the right side of the midline, so that during mating, for example, the apex of the jaws of the male lines up with the left side of the jaws of the female. The presence of injuries and other abnormalities on the jaws of nautilus suggest that similar features on aptychi may have been produced during the normal use of the jaws, and do not necessarily imply an opercular function. Alternatively, aptychi may have served to strengthen and reinforce the lower jaw.

## INTRODUCTION

Aptychi are present in many Jurassic and Cretaceous ammonites, mainly the Ammonitina and Ancyloceratina (Lehmann, 1980; Engeser and Keupp, 2002; Tanabe and Landman, 2002; Landman et al., 2006). Aptychi are pairs of calcitic plates that cover the outside surface of the outer lamella of the lower jaw (Figure 1A). Traditionally, aptychi have been interpreted as opercula (Trauth, 1927–1936; Schindewolf, 1958; Seilacher, 1993; Keupp, 2007), but the discovery of aptychi with other elements of the buccal mass demonstrated their homology with the lower jaws of present-day cephalopods (Lehmann, 1975, 1980). Nevertheless, the opercular theory has never been completely discarded, and as a compromise, Lehmann and Kulicki (1990) have suggested a double function, with aptychi serving as both jaws and opercula. According to these authors, the aptychus was capable of rotating into a nearly vertical position to act as an operculum in the event of an attack by a predator.

The main pieces of evidence for the interpretation of aptychi as opercula are (1) the close match between the size and shape of the aptychus and the aperture of the ammonite, 2) the calcitic composition and ornamentation of the apytchus, suggesting a protective function, and (3) the presence of repaired injuries on the aptychus. Such injuries have been interpreted by Engeser and Keupp (2002) as resulting from predatory attacks. This assertion implies that injuries are only present on opercula, not jaws. The protective function of opercula in gastropods is well known (see, for example, Vermeij and Williams, 2007, and references therein).

In order to evaluate the significance of repaired injuries on aptychi, we studied the externally shelled cephalopod nautilus to determine if repaired injuries or other abnormalities are present on the jaws of these animals. The function of the jaws in nautilus is known. They serve for biting and tearing food. An opercular function is performed instead by the fleshy hood, which is composed of thick connective tissue. The presence of repaired injuries on the jaws of nautilus would imply that injuries, by themselves, are not sufficient proof of an opercular function. Such injuries could equally result from trauma to the jaws during the lifetime of the animal.

The presence of injuries on nautilus jaws also provides insights into the ecology of these reclusive organisms. Because of the deep water habitat of nautilus, direct observations of their behavior are problematic. As a result, investigators have relied on indirect evidence, including analyses of the isotopic

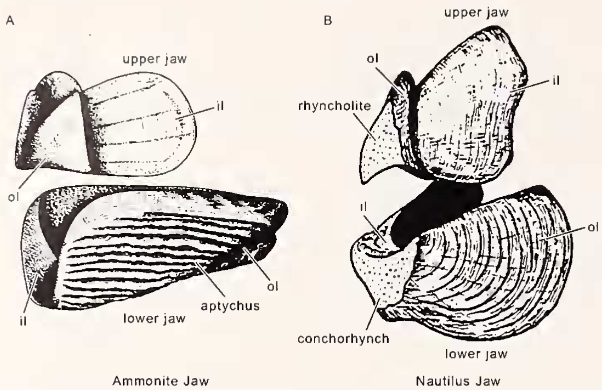


Figure 1. Comparison of the jaws of ammonites with those of modern nautilus. A. Reconstruction of the upper and lower jaws of the Early Jurassic ammonite *Hildoceras* (after Lehmann, 1975: fig. 4). Note that the lower jaw is covered with a pair of calcareous plates, known as an aptychus. il = inner lamella; ol = outer lamella. B. Upper and lower jaws of nautilus (after Tanabe and Fukada, 1999: fig. 19.3). The tips of the jaws are reinforced with calcareous deposits. il = inner lamella; ol = outer lamella.

composition of the shell (e.g., Cochran et al., 1981) and studies of repaired injuries (e.g., Arnold, 1985), for clues about their life history and habitat,

## MATERIAL AND METHODS

The upper and lower jaws of nautilus are composed of chitin and each consists of inner and outer lamellae (Figure 1B). The upper jaw sits inside the lower jaw. The oral opening is surrounded by the labial margin ("lips"). The outside surfaces of the outer lamellae of the upper and lower jaws are mostly covered by a thin membrane of connective tissue and epithelium (Tanabe and Fukuda, 1999). In contrast, the inside surface of the outer lamella and the outside surface of the inner lamella of the lower and upper jaws are covered with muscles. The jaws are reinforced with calcareous deposits at the apex, known as rhyncolites and conchorhynchs (for a more complete discussion of the orientation and terminology of nautilus jaws, see Saunders et al., 1978).

We studied 219 pairs of nautilus jaws in the collections of the American Museum of Natural History (AMNH). All of the jaws are presumably from adult specimens. Part of the sample (164 specimens) consisted of the entire buccal mass preserved in alcohol. The other 55 pairs of jaws were already separated from the buccal mass and subsequently dried. In the alcohol preserved specimens, the upper jaws were still covered by tissue and were not examined for marks. However, in the dried specimens, both the upper and lower jaws were inspected. The jaws belong to four species of Nautilus: 141 jaws of *Nautilus macromphalus* from New Caledonia (57 males, 44 females, 40 *indet.*); 34 jaws of *Nautilus belauensis* from Palau; 42 jaws of *Nautilus pompilius* from various localities (3 from Samoa, 4 from Indonesia, 3 from Fiji, 24 from Papua New Guinea, 8 from the Philippines); and 2 jaws of *Allonautilus scrobiculatus* from Papua New Guinea.

In addition to repaired breaks, we recorded the presence of other abnormalities on the jaws. Specimens were analyzed under the stereomicroscope (x6–x50) and six specimens were observed with SEM. Because of the loss of flexibility of the chitin after drying, some parts of the jaws were broken. These breaks were easy to recognize because of the freshness and sharpness of the fractures.

## RESULTS

### Description of Abnormalities

We categorized the abnormalities observed on the nautilus jaws as follows: (1) repaired fractures, (2) depressions, (3) radial grooves and ridges, and (4) flexures. A total of 149 specimens (68%) of the sample exhibit at least one of these abnormalities. Almost all of the abnormalities occur on the outer lamella of the lower jaw. No abnormalities are present on the upper jaw.

**1) Repaired fractures:** The most spectacular repaired fracture appears on a lower jaw of *Nautilus belauensis* (AMNH 51881). The jaw is 39 mm long and is undoubtedly from an adult specimen. The injury occurs on the left side of the outer lamella and extends from the anterior dorsal part of the wing to the posterior ventral part (Figure 2A, B). The break continues onto the inner lamella (Figure 2C). The outside of the outer lamella is fractured, with a maximum offset of 1.3 mm on each side of the break. On the inside of the outer lamella, the fracture is repaired by an elongate, cordlike thickening of chitin (Figure 2C, D). This chitinous thickening is 2.2 mm wide and 1.0 mm high and subdivides for part of its length. There are no growth lines on the thickening and the texture is reminiscent of pahoehoe lava.

**2) Depressions:** Small depressions are present on some of the nautilus jaws (Figure 3C–F, I, J). These features only occur on the outside of the outer lamella of the lower jaw. Several depressions may occur on the same specimen (Figure 3E, F). The depressions are less than 1 mm long and less than 0.2 mm deep. They vary in shape from triangular to quadrate to round. They are conformable with the surrounding jaw surface, but show a slightly different texture. The depressions are not expressed on the inside surface of the outer lamella. They occur in all of the nautilus species but are more common in *Nautilus pompilius* and *N. belauensis*. They preferentially occur on the left side of the outer lamella in these species.

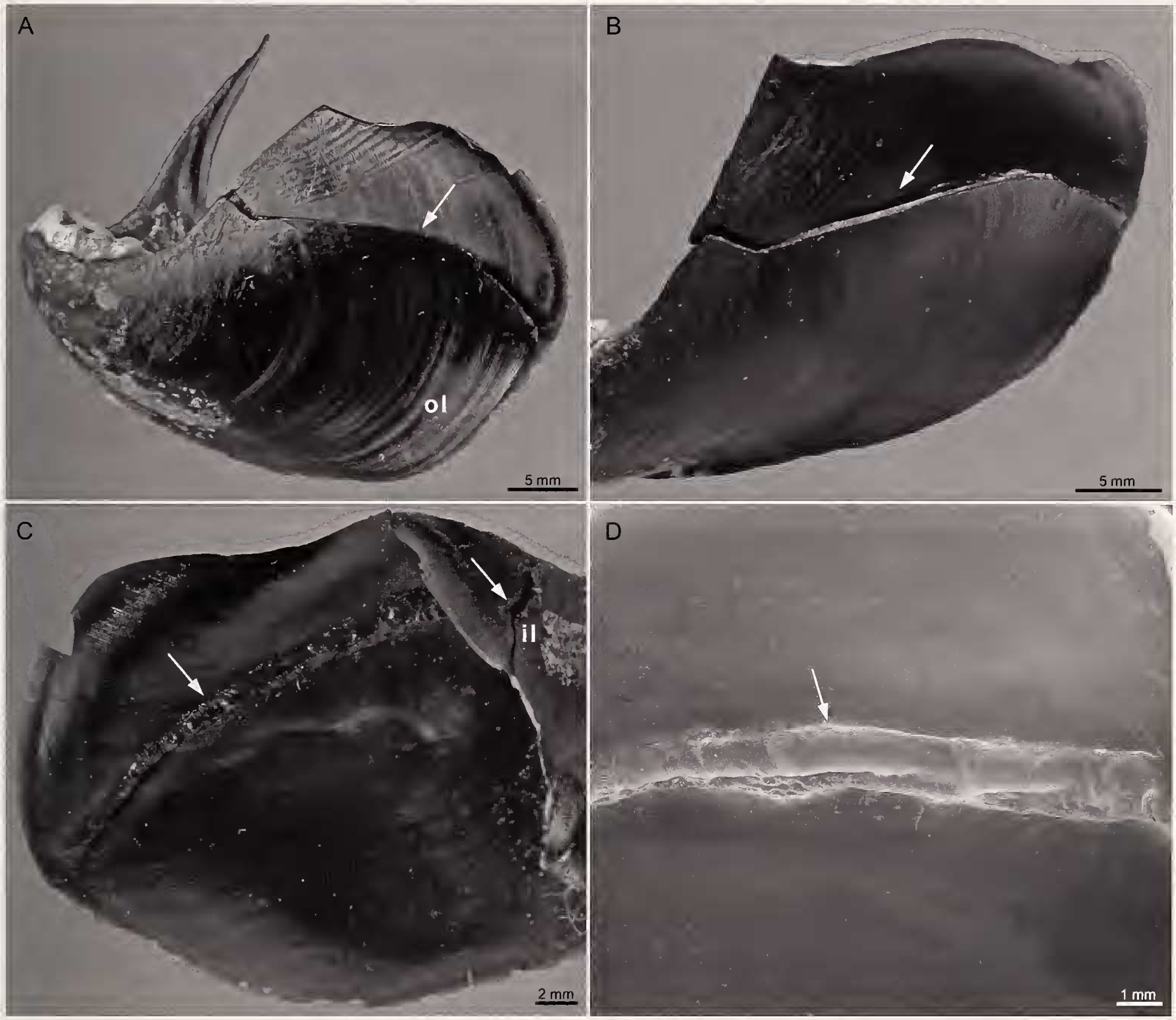


Figure 2. Lower jaw of *Nautilus belauensis* (AMNH 51881) with a large repaired injury. A. Left lateral view of the lower jaw, showing the break (arrow) on the outer lamella (ol). The break extends to the posterior end of the wing. Part of the calcareous deposit at the tip was broken away during handling. Anterior direction to the left. B. Left lateral view of the lower jaw, slightly tilted down, to expose the gap at the break (arrow). C. View of the inside surface of the outer lamella, showing the repaired portion (left arrow). Note that the break (right arrow) continues onto the inner lamella (il). Anterior direction to the right. D. Close-up of the repair (arrow) on the inside surface of the outer lamella, which consists of a thickened ridge of chitin that must have been secreted from the inside.

**3) Radial grooves and ridges:** As noted by Saunders et al. (1978), the outside surface of the outer lamella of the lower jaw is covered with closely spaced, comarginal lirae, which are usually interpreted as growth lines. In some specimens, however, these growth lines are transected by elongate grooves that occasionally extend to the posterior margin (Figure 3A, B). These grooves are generally superficial with a maximum depth of approximately 0.2 mm, and are usually bordered by thin ridges. Sometimes, instead of grooves, the surface is marked by thin bands, approximately 0.5 mm wide, characterized by an irregular texture (Figure 3G, H). Radial grooves or bands occur in 54% of the specimens that show abnormalities.

**4) Flexures:** Flexures are minor discontinuities in the outer lamella of the lower jaw, which follow the course of the lirae (Figure 3K, L). They are sometimes expressed as overhanging fringes of chitin, indicating the previous position of the jaw margin. Flexures are very common and preferentially occur on the left side of the lower jaw (92% of the specimens with flexures).

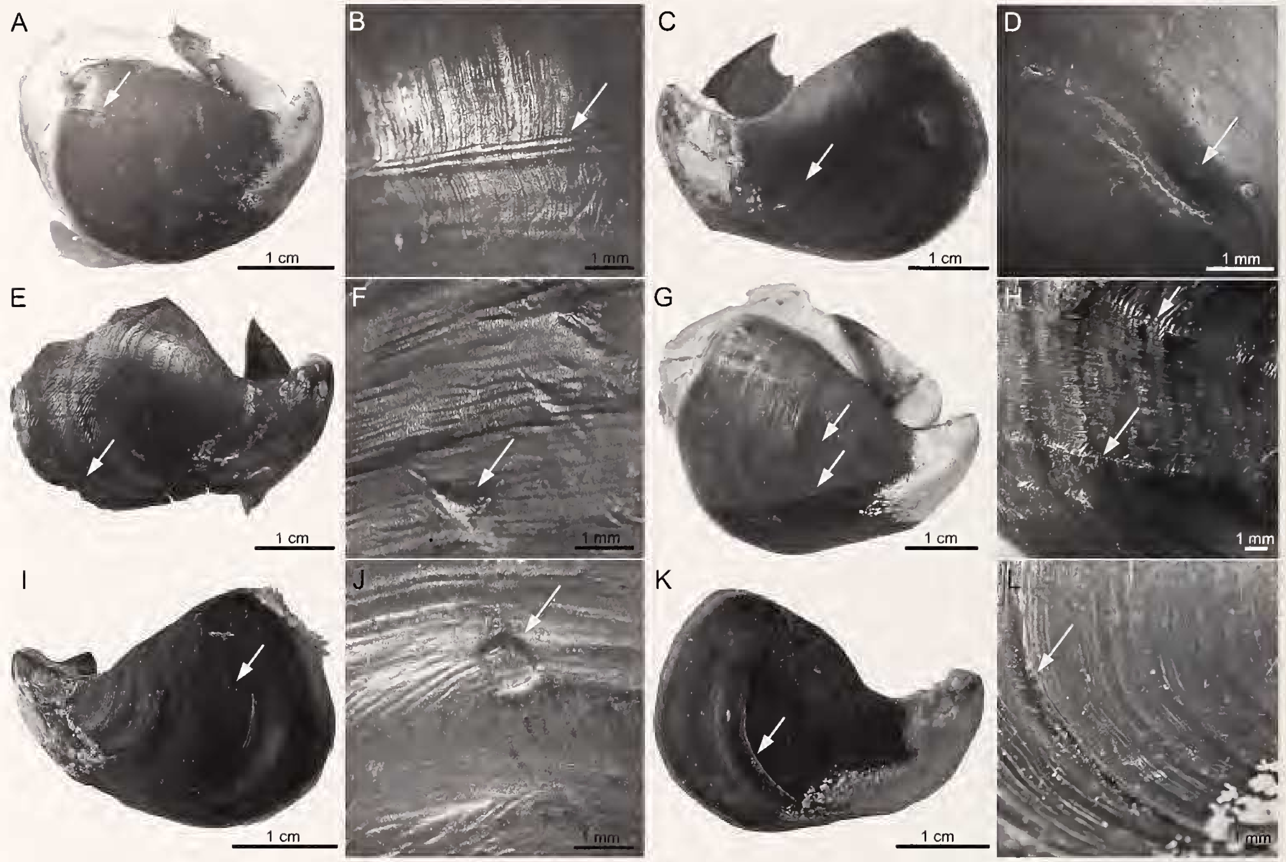


Figure 3. Abnormalities on the lower jaws of nautilus. A, B. Radial groove (arrow) on the outer lamella of the lower jaw of *Nautilus macromphalus* (AMNH 51870). The groove extends to the posterior margin of the wing, suggesting permanent damage to the jaw-secreting tissue. Anterior direction to the right. The close-up in B is rotated 180° relative to A. C, D. Elongate depression (arrow) on the outer lamella of the lower jaw of *Nautilus belauensis* (AMNH 51868). Anterior direction to the left. E, F. Triangular depression (arrow) on the outer lamella of the lower jaw of *Nautilus belauensis* (AMNH 51335). Anterior direction to the right. G, H. Radial bands (arrows) on the outer lamella of the lower jaw of *Nautilus belauensis* (AMNH 51883). Anterior direction to the right. I, J. Small depression (arrow) on the outer lamella of the lower jaw of *Nautilus pompilius* (AMNH 51869). Anterior direction to the left. The close-up in B is rotated 180° relative to I. K, L. Flexure in the chitin (arrow) on the outer lamella of the lower jaw of *Nautilus macromphalus* (AMNH 51884). Anterior direction to the right. The calcareous tips of the jaws are occasionally missing in these specimens due to breakage during drying or handling.

## Distribution of Abnormalities

The incidence of abnormalities varies among the different species. The highest percentage of abnormalities occurs in *Nautilus belauensis*, including the specimen with the conspicuous scar. The highest percentage of grooves appears in *N. macromphalus*. The percentage of depressions is higher in *N. belauensis* and *N. pompilius* than in the other species. In *N. macromphalus*, in which the number of males and females is known, the incidence of abnormalities is higher in males than in females (70% versus 55%). The most common abnormality in both sexes is grooves. However, the incidence of grooves is higher in males than females (60% versus 36%).

Some of these differences may be related to the preservation of the jaws (alcohol versus dry). For example, most of the flexures occur in alcohol-preserved rather than dry specimens (92% versus 8%), perhaps because flexures are less noticeable on dry specimens. In contrast, depressions are more common on dry specimens. Therefore, the kind of preservation may bias the results.

## DISCUSSION

The abnormalities described on the jaws of nautilus are either the result of injuries to the jaws or growth pathologies. The repaired break in AMNH 51881 is the most obvious example of a repaired injury in which the lower jaw was broken and repaired during life by the secretion of additional chitinous material from the inside. The depressions, with a maximum depth of 0.2 mm, may also represent injuries due to impact, or possibly damage caused by parasites. In any event, the damage was not permanent. In contrast, the radial grooves and ridges extending to the posterior margin of the jaws imply permanent damage to the jaw-secreting tissue, perhaps due to injury. The flexures that follow the growth lines probably represent pauses in growth due to stress, after which growth resumed, and are not related to injuries to the jaws.

The injuries on these jaws may be due to several factors. They may have been produced during feeding. In their natural habitat, nautilus regularly feed on crustaceans (Saunders and Ward, 1987; Saunders et al., 1987; Ward, 1987), as confirmed by reports of crustacean remains in the gut contents of freshly captured nautilus (Haven, 1972). In addition, Ward and Wicksten (1980) observed *Nautilus macromphalus* in captivity eating freshly molted exoskeletons of lobsters. Thus, the nautilus may have damaged their jaws by simply biting down on a hard crustacean carapace. Injuries may also have been caused by counterattacks of the prey. For example, Ward (1981) observed hermit crabs defending themselves against nautilus attack by breaking off pieces of the nautilus shell.

Alternatively, the injuries on nautilus jaws may have been produced by predators. The large breaks observed on nautilus shells have routinely been attributed to predators such as teleosts, sharks, and crabs (Arnold, 1985; Ward, 1987). There are few eye witness accounts of predatory attacks, but Saunders et al. (1987) observed such an attack by triggerfish on *Nautilus belauensis* in shallow water in Palau.

Another possible source of injuries on nautilus jaws may be linked to mating and courtship behavior. During copulation, a male nautilus grasps the shell of the female (Arnold, 1985, 1987), and the jaws of both sexes could be damaged in the process. The jaws of the male are especially vulnerable to counter attack by the female if the male is using its jaws to grasp the shell of the female. Injuries could also be produced during fights between males. Haven (1972) noted bites in the hoods and V-shaped breaks in the shells of *Nautilus pompilius* in captivity, which she attributed to combat between males. This behavior is consistent with the observation that in our sample of *N. macromphalus*, in which the distribution of sexes is known, jaw abnormalities are more common in males than females.

The location of the abnormalities sheds some light on the biology of nautilus. Nearly all of the abnormalities occur on the outer lamella of the lower jaw. Because the upper jaw is mostly covered by muscles and sits within the lower jaw, the outer lamella of the lower jaw is more vulnerable to injury. Furthermore, most of the abnormalities occur on the left side of the lower jaw. This pattern may be related to the position of the jaws in the shell. In males, the jaws are displaced toward the right side of the shell due to the development of the spadix (Saunders and Spinosa, 1978; Saunders and Ward, 1987). Thus, during copulation, the apex of the jaws of the male lines up with the left side of the jaws of the female and, conversely, the apex of the jaws of the female lines up with the left side of the jaws of the male. This offset has also been cited to explain the disparity in the incidence of repaired shell breaks between the left and right sides of the shell. For example, Arnold (1985) noted that, in females, there is a higher incidence of injuries on the left side of the shell. The off-center position of the jaws in males also implies that, during male to male combat, the left side of the jaws is more vulnerable to damage than the right side.

The highest percentage of abnormalities occurs in *Nautilus belauensis*. This probably reflects the larger size of the jaws of this species. With more surface area to inspect, the probability of finding injuries is higher. In addition, studies of the longevity of nautilus suggest that *N. belauensis* is longer lived than the other nautilus species (Landman and Cochran, 1987). Because of their longer life span, these animals may have had a greater chance of sustaining injuries.

The paleontological implications of our observations bear on the arguments used to support the opercular theory of ammonite aptychi (Seilacher, 1993; Keupp, 2007). Traditionally, irregular marks on aptychi have been interpreted as healed injuries and, thus, proof of an opercular function. There are many illustrations of such marks on aptychi from the Jurassic of Germany (for example, Schindewolf, 1958: pls. 5, 9; Keupp et al., 1999: pl. 3, fig. 6; Keupp, 2000: 114, upper left; Engeser and Keupp, 2001: fig. 2). In addition, Landman et al. (2007: figs. 13.17–20) have illustrated such marks on the aptychi of *Baculites* from the Upper Cretaceous of North America.

Our study of abnormalities on nautilus jaws suggests that the formation of such features on aptychi may have been the result of the normal use of the jaws. However, we cannot exclude the possibility of an opercular function, although this interpretation requires more evidence. Alternatively, the aptychi may have simply served to strengthen the lower jaw. In this context, it is worth noting that nearly all of the abnormalities that we observed on nautilus jaws appear on the outside surface of the outer lamella of the lower jaw. Thus, the thick calcareous plates comprising the aptychus may have functioned to protect the outer surface of the lower jaw in ammonites, even if the aptychus did not rotate into a vertical position, as envisioned by Lehmann and Kulicki (1990).

## FUTURE WORK

This is the first study of abnormalities on nautilus jaws (or any cephalopod jaws, for that matter). Further studies could investigate the relationship between injuries on the nautilus shell and those on the jaws. Is an injury on the shell also expressed on the jaws? Such studies might provide additional insights into the ecology and behavior of nautilus—that is, their prey and their predators. It would also be interesting to determine if there are geographic differences in the occurrence of jaw injuries associated with different feeding habits.

From the paleontological point of view, our study suggests the need to more carefully examine the abnormalities on ammonite aptychi. Are these marks, in fact, the same as those on nautilus jaws? Do they appear on the inner and outer sides of the aptychus or only on the outer side? Do the injuries extend to the underlying chitinous layer of the jaw or are they restricted to the calcareous plates? The extent to which the marks on aptychi are the same as those on the jaws of nautilus will determine the extent to which our observations about nautilus can shed light on the functional interpretation of ammonite jaws.

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